

INVASION AND SPREAD OF *CALLITRICHE STAGNALIS*
(CALLITRICHACEAE) IN NORTH AMERICA

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ABSTRACT. *Callitriche stagnalis* (Callitrichaceae) is a widespread aquatic species in the Old World, but an adventive component of the North American flora. Herbarium records are used to document the historical and current distribution of *C. stagnalis* in North America. It is hypothesized that the species initially established in North American seaports. The earliest collections of *C. stagnalis* in North America are from coastal regions in New York (1861), Oregon (1871), and New Jersey (1885). Prior to 1925, it is known from only a single noncoastal location (Montana, 1898). The rate of spread of *C. stagnalis* on the east versus west coast of North America differs. The species was well established on the east coast by the 1920s in New Jersey, New York, and southeastern Pennsylvania. On the west coast, only two locations (Oregon, British Columbia) were known by this time. The current distribution indicates that the species has spread about the same distance in both east and west coastal regions (400–500 miles): west coast, from the first documented locality in Clatsop Co., Oregon, to Napa Co., California, and east coast from Mercer Co., New Jersey, to regions of the St. Lawrence River in Quebec. Inland populations (Alabama, Montana, Wisconsin) are anomalous. Seed production is prolific in *C. stagnalis* and seeds are likely the principal unit of dispersal.

Key Words: *Callitriche stagnalis*, aquatic plants, nonindigenous species

Many species in the aquatic and wetland flora of North America are nonindigenous, having invaded from other regions (e.g., Les and Stuckey 1985; Stuckey 1966, 1970, 1974, 1979, 1980, 1981, 1985, 1993; Stuckey and Phillips 1970). These species new to an area or region are immigrants or invasive species that are

often referred to as foreign, alien, or exotic members of the flora (Stuckey and Barkley 1993). Foreign plants can have drastic impacts on the ecology of aquatic and wetland environments, as exemplified by *Lythrum salicaria* L. (Lythraceae, cf. Stuckey 1980) and *Myriophyllum spicatum* L. (Haloragaceae, cf. Pieterse and Murphy 1993). However, most alien plant species have remained rather inconspicuous. Examples of the latter include *Lycopus europaeus* L. (European water-horehound; Stuckey and Phillips 1970) and *Veronica beccabunga* L. (European brooklime; Les and Stuckey 1985). Though not troublesome from a human perspective, it remains unknown what impact these exotic species may have on wetland plant communities and the ecology of wetland environments.

Callitriche stagnalis Scop. (water starwort) is a widespread aquatic plant of Europe, northern Africa (Clapham et al. 1987; Schotsman 1954, 1961a, b, 1967, 1972; Schotsman and Andreas 1980), Asia, Australia, New Caledonia, and New Zealand (Mason 1959). The species occurs in diverse aquatic and subaquatic habitats, e.g., marshes, stream and pool margins, and low, wet areas. Schotsman (1954, 1961a, b, 1972, 1985) has published works on various aspects of the taxonomy, biology, and distribution of the species in Europe.

The distribution of *Callitriche stagnalis* has evidently expanded considerably via human activities, and this species now seems to be the most widespread in the genus. Since the early part of this century it has been recognized that *C. stagnalis* is an adventive component of the North American flora. *Callitriche stagnalis* is readily distinguished from other amphibious species of *Callitriche* in North America (e.g., *C. heterophylla* Engelm. ex Hegelm. and *C. verna* L. emend. Kütz.) by its nearly round fruits in outline and the broad marginal wing that extends from the apex to around the base of each mericarp.

Fernald (1932), Rousseau (1968), and Svenson (1932) published brief accounts of the regional distribution of the species in eastern North America. Fassett (1951), in his revision of *Callitriche* in the New World, provided information on the distribution of the species in North America. Numerous specimens, however, that document a much wider distribution were evidently overlooked by Fassett. In addition, the species has spread considerably since the time of Fassett's paper.

The purpose of this paper is to use herbarium specimens to

document the spread of *Callitriche stagnalis* in North America. Three questions are addressed: 1) When and where was *C. stagnalis* first documented in North America? 2) How has the distribution of the species expanded subsequently? 3) What is the current distribution of the species?

MATERIALS AND METHODS

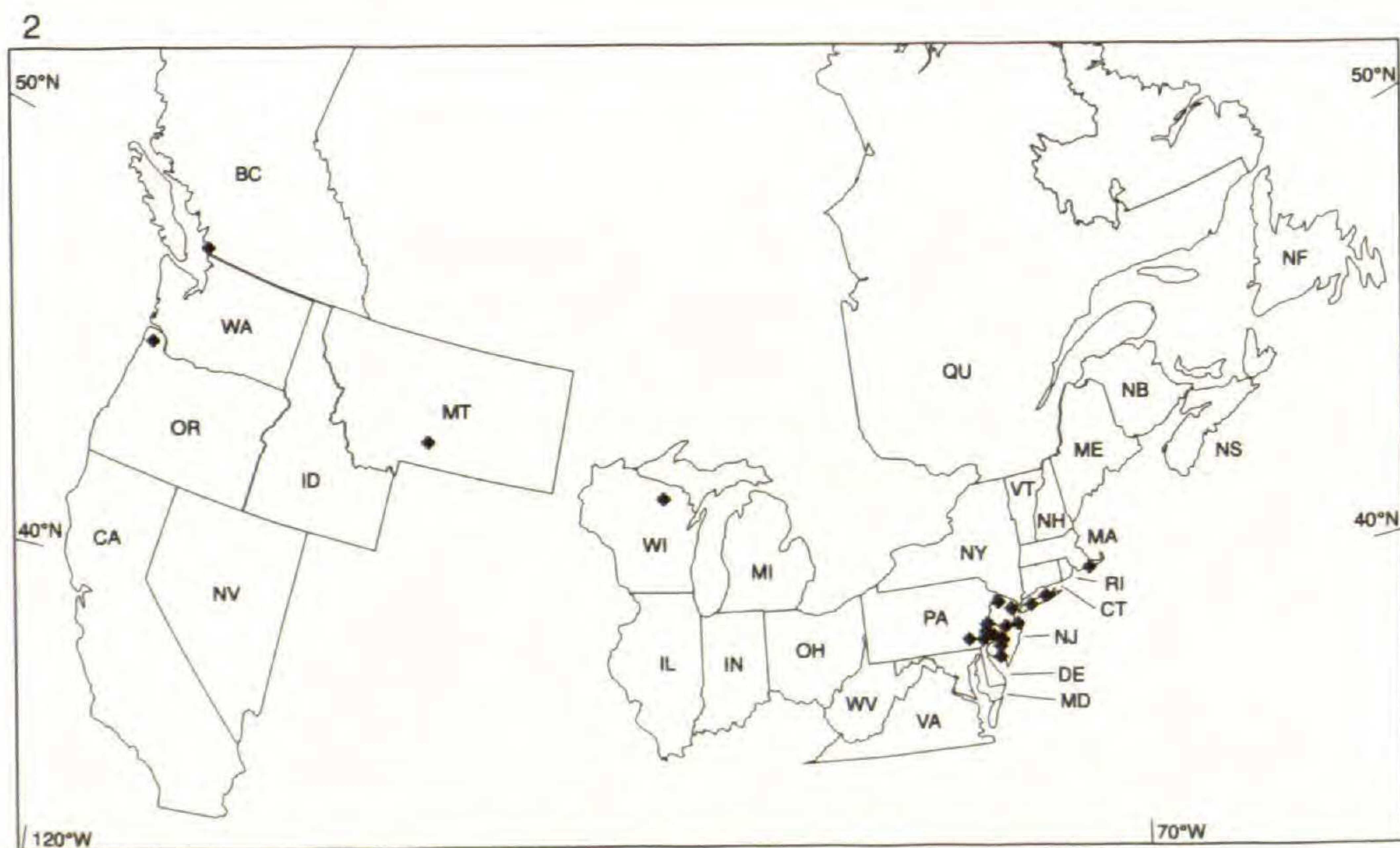
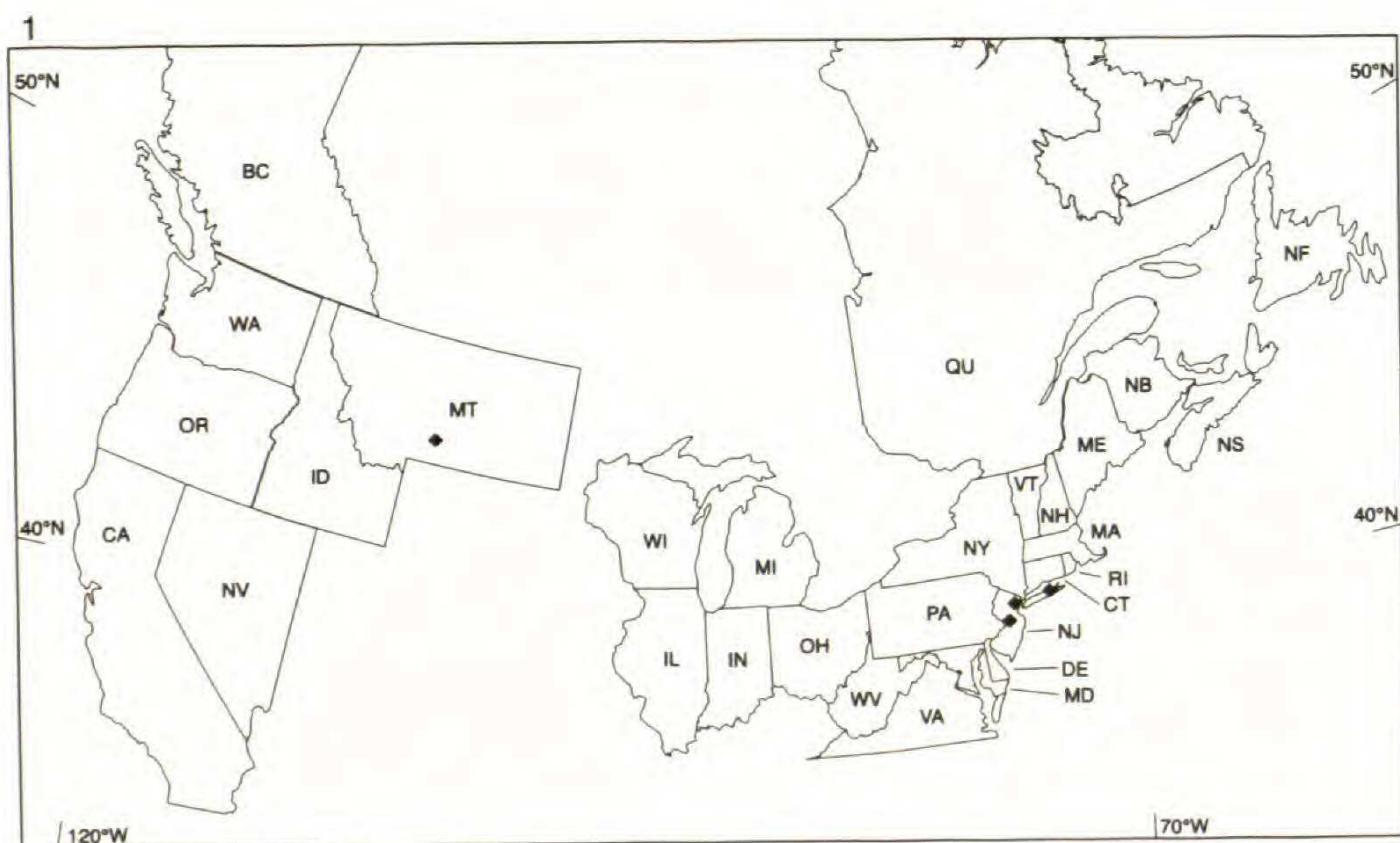
This study is based on examination of specimens from the following herbaria: ALA, ALTA, ARIZ, CAS, CLEMS, COLO, CONN, CU, F, FLAS, GH, IND, JEPS, KANU, KNK, LL, MAINE, MICH, MIN, MO, MT, NCU, NEBC, NHA, NY, OS, PH, RM, ROMO, RSA/POM, TEX, TRT, UBC, UNA, US, USFS, WCSU, WIS, WTU. It is difficult to confidently identify specimens of *Callitriche stagnalis* that lack fruit. Only specimens that have fruits are included in this study. Representative specimens that document the distribution are illustrated in Figures 1–4 and listed in Appendix 1.

The maps illustrate the distribution of *Callitriche stagnalis* for four periods: prior to 1900 (Figure 1), prior to 1926 (Figure 2), prior to 1951 (Figure 3), and current (Figure 4). These periods were selected to illustrate the progressive expansion of the species. The distribution maps are based exclusively on specimens examined, not on the published literature, although the latter is discussed in the text when relevant.

RESULTS

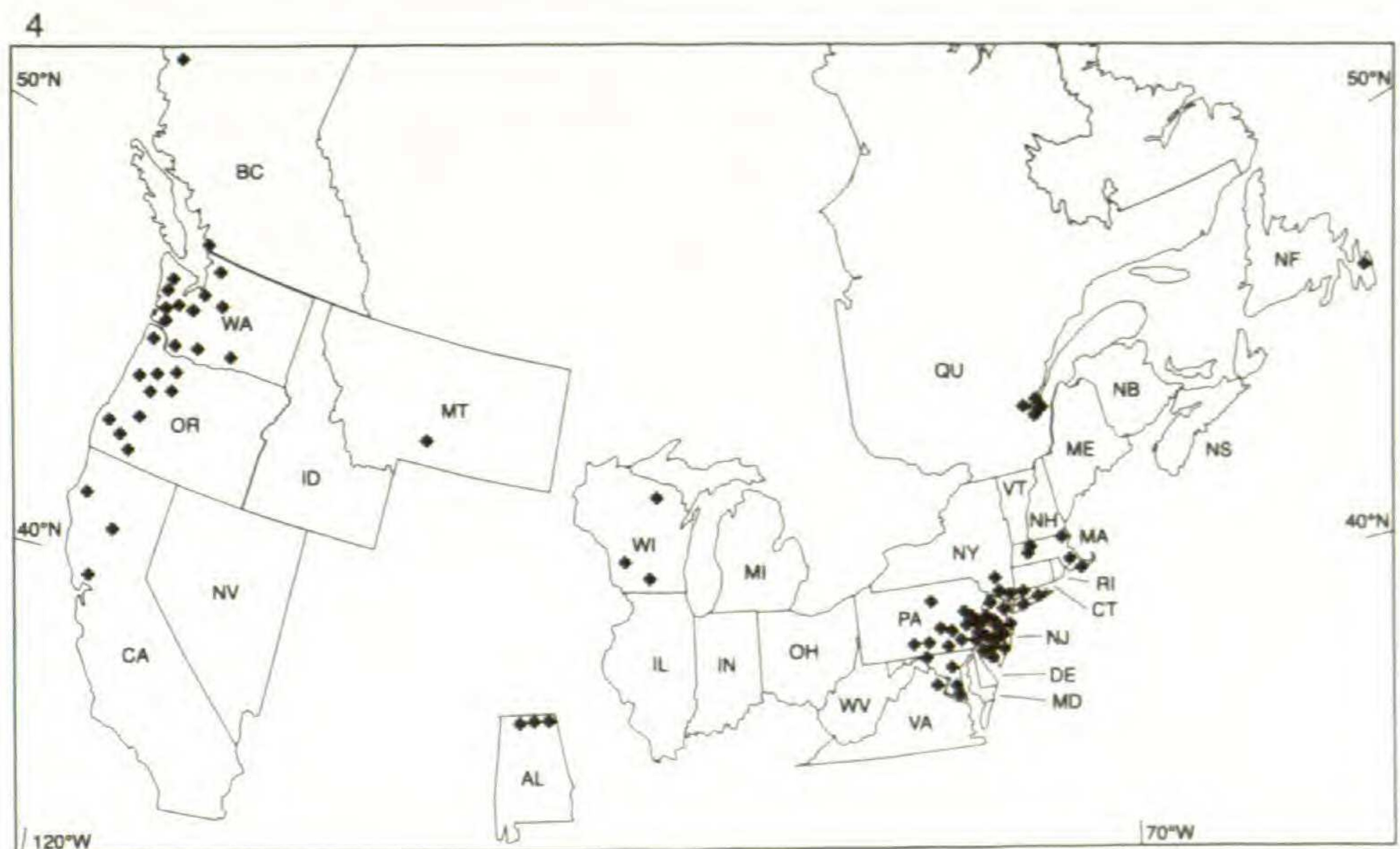
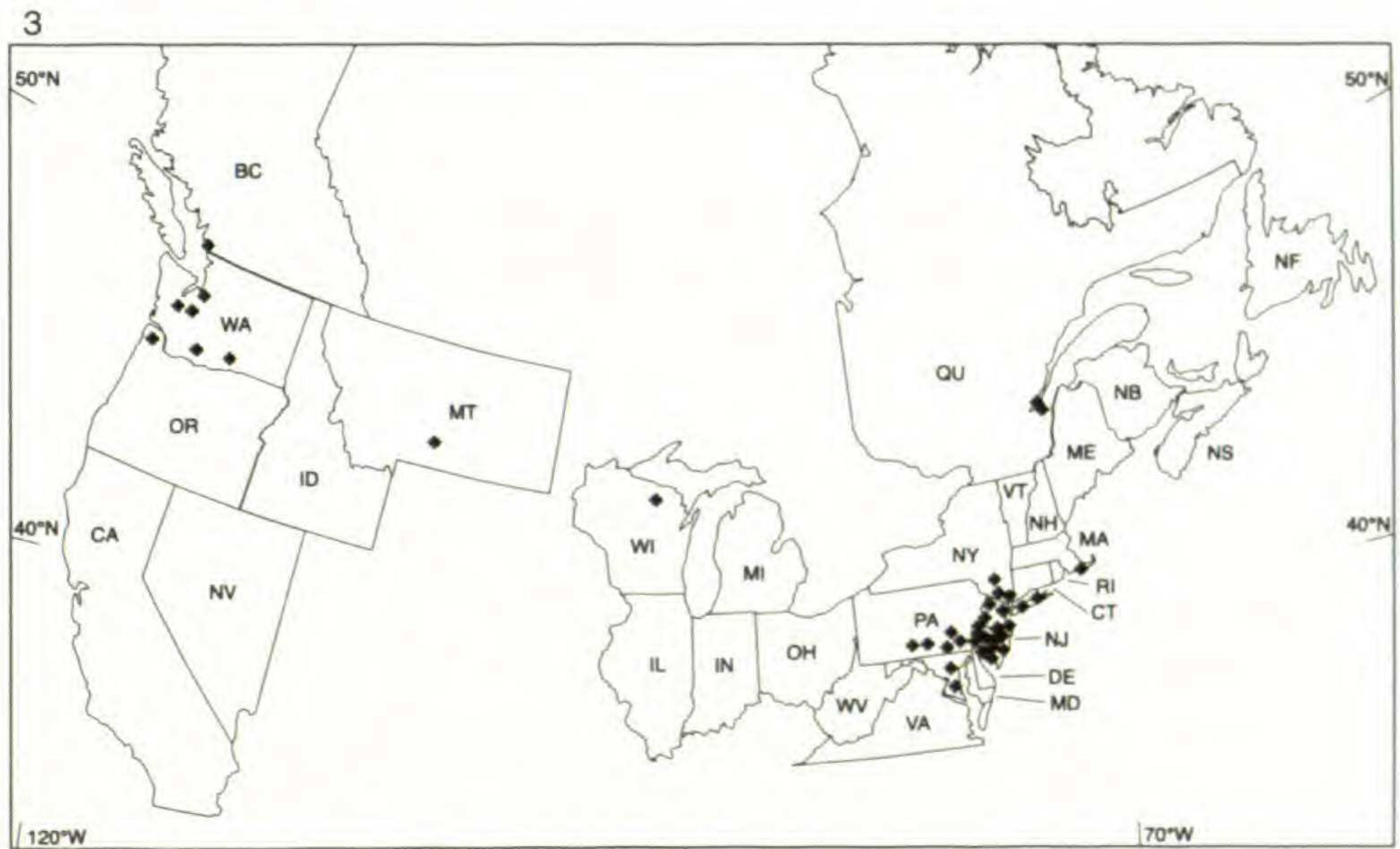
The earliest collection of *Callitriche stagnalis* in North America (1861) is from the state of New York (Figure 1; Appendix 1) although the locality from which it was collected is not known. An early collection without locality also exists from Oregon (1871). Interestingly, an early (1898) noncoastal location from Montana is also documented. Herbarium records further document that prior to 1900 the species occurred in New Jersey (Mercer Co., 1885; Bergen Co., 1891; Figure 1; Appendix 1). The first collection that can be attributed to a specific locality is from Suffolk Co., New York (Long Island, 1898; Appendix 1).

By 1925, the species is documented from 12 additional counties in eastern North America (Figure 2; Appendix 1): in New Jersey (Passaic Co., 1901; Camden Co., 1905; Gloucester Co., 1910; Cumberland Co., 1923; and Monmouth Co., 1923), New



Figures 1–2. Distribution of *Callitriche stagnalis* in North America (see Appendix 1). Selected regions of the United States and adjacent Canada are shown. Each diamond represents the first documentation for a county (U.S.) or region. Collections from New York (1861) and Oregon (1871) are not shown (see text). U.S. states and Canadian provinces are identified by postal abbreviations. 1. Collections prior to 1900. 2. Collections prior to 1926.

York (Nassau Co., 1926), and Massachusetts (Barnstable Co., 1911), in addition to five counties in Pennsylvania (Delaware Co., 1911; Montgomery Co., 1922; Philadelphia Co., 1923; Bucks Co., 1923; Chester Co., 1924). By 1925, the species is also doc-



Figures 3–4. Distribution of *Callitriche stagnalis* in North America (see Appendix 1). Selected regions of the United States and adjacent Canada are shown. Each diamond represents the first documentation for a county (U.S.) or region. 3. Collections prior to 1951. 4. Collections to present. Alabama is included in this figure but not in Figures 1–3.

umented from locations on the west coast of North America (Oregon, Clatsop Co., 1902, and British Columbia, New Westminster, 1916) and from an inland location in Wisconsin (Oneida Co., 1925), in addition to Montana.

Herbarium specimens indicate that by 1950 the distribution of *Callitriche stagnalis* had expanded considerably in the northeastern United States to include populations in four additional counties in New York and Pennsylvania and seven additional counties in New Jersey (Figure 3). In addition, two records in Maryland document the species for the first time in that state (Montgomery Co., 1942; Prince George's Co., 1943) and soon after (1952) in Virginia. Between 1926 and 1950 the species is also documented from four localities along the St. Lawrence Seaway in Quebec. Similarly, by 1950 specimens document the spread of the species in the northwestern United States (Washington: Benton Co., 1926; King Co., 1933; Pierce Co., 1934; Thurston Co., 1942; Yakima Co., 1942) and British Columbia (the region of Vancouver).

By the 1970s, the species had spread into the northernmost location from where it is currently documented on the east coast in Newfoundland (1968) and in states where it had previously been documented (Figure 4; Appendix 1). The northernmost location for the species on the west coast is from the Skeena River, British Columbia (Figure 4). Particularly notable are the records for the species occurring in three additional counties in Massachusetts, five in Pennsylvania, three in Washington, and two in Wisconsin. During this period it is documented from the southern United States (Alabama: Limestone, Madison, and Jackson Counties) as well as in California (Figure 4; Appendix 1).

The current distribution of *Callitriche stagnalis* (Figure 4) spans from Maryland to Massachusetts (one locality in Newfoundland, Canada) on the eastern seaboard, and more than 100 miles inland, especially in Pennsylvania. On the west coast the species is especially common in western parts of Oregon and Washington and in some areas of southwestern mainland British Columbia and Vancouver Island. In California it occurs in northern portions of the Central Valley and in the northern coastal region.

DISCUSSION

We interpret the data from herbarium specimen documentation as indicating that *Callitriche stagnalis* is not native to North America. Herbarium specimens document a progressive expansion of *C. stagnalis*, primarily in east and west coastal regions of North America, subsequent to invasion of the species circa the

1850s. The pattern observed for *C. stagnalis* is similar to that reported for numerous other wetland plant species (Stuckey 1993, and references therein).

Several authors reported on the early distribution of *Callitriche stagnalis* in North America. Svenson (1932) noted that *C. stagnalis* was a component of the northeast flora since at least 1905, citing specimens from Massachusetts, New York, New Jersey, and Pennsylvania. Fernald (1932) reported the species “while collecting on the always interesting tidal flats of the lower St. Lawrence” in Quebec. Fassett’s (1951) account of the distribution of *C. stagnalis* was more thorough, although he evidently was not aware of specimens that documented an even broader distribution. Muenscher (1944) included Michigan on his map of the species, although no specimens have been documented in that state. Voss (1985) does not list this species in his flora of Michigan. Warrington (1980) reported the species from three areas in British Columbia: Vancouver, the region of Shuswap Lake (5 locations), and three locations on Vancouver Island. Specimens that may document the species on Vancouver Island were not seen by the authors. Fassett (1951) suggested that the early (1871) collection from Oregon might indicate that the species is native to that region. Although Cook (1985) listed the species as “questionably introduced” in North America, we contend that the data presented here confirm its non-native status.

Stuckey (1993) included *Callitriche stagnalis* in a general pattern of nonindigenous aquatics from Europe that occur primarily in the northeastern United States and eastern Canada, as well as the northwestern United States and adjacent Canada. Examples of other species that show similar patterns include *Lythrum salicaria*, which has become a troublesome invasive species, in addition to the less conspicuous *Butomus umbellatus* L., *Epilobium hirsutum* L., and *Veronica beccabunga*.

From the data presented herein it is evident that *Callitriche stagnalis* has undergone range expansion since first invading coastal regions. The species apparently arrived early in northern New Jersey, New York, and Oregon. Considerable regional expansion is evidenced in the mid-Atlantic states and Pacific Northwest. Currently, *C. stagnalis* exhibits its widest distribution in coastal regions in North America.

Knowledge of the invasions, subsequent spread, and establishment of alien species is valuable when making predictions of

future distributions and possible ecological impact on native species. Several possible scenarios can explain the invasion and spread of *Callitriche stagnalis* in North America. Because this species is documented primarily from coastal regions during the first 60 years of its occurrence, a probable location of invasion is at seaport cities, where it may have arrived via ship ballast. Invasions of foreign species into coastal regions and subsequent migration inland have been reported for other aquatic and wetland species, among them *Lythrum salicaria* (Lythraceae; Stuckey 1980), *Rorippa sylvestris* (L.) Besser (Brassicaceae; Stuckey 1966), *Lycopus europaeus* (Lamiaceae; Stuckey and Phillips 1970), and *Veronica beccabunga* (Scrophulariaceae; Les and Stuckey 1985).

The number of times *Callitriche stagnalis* entered North America is not clear. Because invasions are a result of stochastic, largely unpredictable events, single and multiple introduction scenarios are equally probable. The species was present in both the northeast (New Jersey, New York) and northwest (Oregon) by the 1880s. It is possible that the species invaded twice, once on each coast. A single invasion into New York and subsequent spread (perhaps via shipping between east and west coasts) is also possible. Studies of the nature of the shipping industry during this time and the types of commerce taking place between these regions could provide a means of substantiating possible scenarios. Spread to new regions from earlier established populations or additional invasions could be invoked to account for subsequent population establishment along the St. Lawrence River in Quebec and perhaps in northern New York. The use of genetic markers (e.g., isozymes; cf. Soltis and Soltis 1989) could provide insight on the number of invasions as well as patterns of subsequent spread.

With the majority of the current distribution in coastal regions, the inland populations (Alabama, Montana, Wisconsin) of *Callitriche stagnalis* are anomalous. It is not possible to assess whether the relatively early (1925) introduction of the species into Wisconsin is a consequence of spread from coastal areas or represents an additional invasion. In northern Alabama the three county locations are along the Tennessee River. These locations may represent spread of the species from other North American locations. No direct link by shipping or other commerce is apparent between this region and Europe that would explain the fairly recent (1980)

documentation. R. Haynes (pers. comm.) suggests that the species may be native to several natural springs in northern Alabama. The early (1898) documentation from Montana could be used to support an argument for the species being native to North America. Interestingly, only a single collection from 1898 documented the presence of *C. stagnalis* in Montana [a specimen (23 Aug 1979, *Lackschewitz* 9219, RM) from Ravalli Co., Montana, lacks fruit but may be *C. stagnalis*]. Although the inland populations are difficult to explain, we feel that the pattern of spread of the species in North America over the last century, documented by herbarium specimens, indicates that it is not native to North America.

The rate of spread of *Callitriche stagnalis* on the east versus west coast seems to differ. Herbarium specimens indicate that the species became well established on the east coast by the 1920s in New Jersey, Long Island (New York), and southeastern Pennsylvania. In contrast, on the west coast, only two locations (Oregon, British Columbia) are documented by this time. Even so, the species has spread about the same distance in both eastern and western coastal regions: west coast, from the first documented locality in Clatsop Co., Oregon, to Napa Co., California, and east coast from Mercer Co., New Jersey, to regions of the St. Lawrence River in Quebec.

Reproductive systems play a central role in the spread of exotic species (e.g., Baker and Stebbins 1965, and references therein). The reproductive biology of *Callitriche stagnalis*, especially in its foreign range, is poorly understood. For example, whether the species grows as an annual or perennial form is dependent upon climate. Martinsson (1991) reported an annual habit for plants grown under greenhouse conditions in Sweden. By inference, the same is also possible for natural populations in that cold climate region. In contrast, the species seems to be perennial in the northeastern United States. One of the authors (Philbrick) has observed green plants along streams in southwestern Connecticut in January. Similarly, Svenson (1932) reported plants as "green and thriving" in midwinter on Long Island (New York), and Fernald (1950) also reported the species as perennial.

The growth form of this amphibious species indicates that it can spread readily within a local area via clonal growth. Plants in shallow water, or on moist soil, exhibit extensive horizontal growth, producing numerous nodal roots and developing a dense

mat of intertwining stems. However, unlike many clonal species of aquatic and wetland plants (Philbrick and Les 1996; Sculthorpe 1967), species of *Callitriche* do not produce specialized vegetative propagules. Dispersal of plant fragments is possible, although their involvement in the geographic spread of the species is not known.

Seed production is prolific in *Callitriche stagnalis* in both its native and adventive (North American) ranges. Seeds seem to be the principal units of dispersal and geographic spread. Philbrick (1989) and Philbrick and Anderson (1992) have shown that the flowering period of *C. stagnalis* in North America ranges from April to November, and seed production is near 100% as geitonogamous pollination (pollination between flowers at a node) predominates. Thus, seed can be produced after a single plant becomes established. Possible means of seed dispersal are not known. Reports exist that seeds of species of *Callitriche* are eaten by ducks (cf. Fassett 1957), although it is not clear what role ducks, or birds in general, play in dispersal (birds' feet?). Human activities may actively transport seeds of *C. stagnalis*. This species often occurs in roadside ditches in Oregon and Washington. Seeds may well be transported in wet mud by vehicle traffic in these regions.

Species of *Callitriche* are not known to be troublesome aquatic weeds. In their book on aquatic weeds, Pieterse and Murphy (1993) consider only one species (*C. verna* in Japan) as being occasionally troublesome. Current observations suggest that *C. stagnalis* will become a nuisance in some regions of North America. Hitchcock and Cronquist (1973) listed the species as being occasional in Oregon, but did not list it as occurring in Washington. Yet, the species is now widespread in the western portions of both states. In Oregon, it seems to be even more widespread than herbarium records indicate (R. Halse, pers. comm.). *Callitriche stagnalis* is now also common in the lower Fraser River Valley in British Columbia (A. Ceska, pers. comm.) and in the region around the city of Quebec (L. Brouillet, pers. comm.). Because the species regularly produces dense clonal stands in irrigation canals and roadside ditches, it will predictably have an impact on native aquatic plant species.

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APPENDIX 1: SPECIMENS OF *CALLITRICHE STAGNALIS* IN CANADA AND THE UNITED STATES THAT DOCUMENT ITS DISTRIBUTION IN A STATE, COUNTY, OR REGION WITHIN A PROVINCE.

Specimens are organized alphabetically by country, and state or province. Only the first documented collection from each county or region within a province is listed. Specimens noted with * have incomplete or unclear label information and are not included in Figures 1–4.

Canada. BRITISH COLUMBIA: New Westminster, 10 Jun 1916, *Henry 9068* (GH); Skeena R., 13 Sep 1974, *Pojar s.n.* (UBC); NEWFOUNDLAND: St. John's Co., 17 Jun 1968, *Scott 219* (UBC); QUEBEC: Bellechasse Co., Bellechasse, 26 Aug 1931, *Victoria & Germai 45062* (CU); Desjardins Co., Lauzon, 1 Aug 1950, *Desmarais 1077* (MT); Quebec metropolitan area, Point Pizeau, 8 Aug 1950, *Desmarais 1881* (MT); I'le d'Orleans Co., St. Pierre, 25 Jul 1936, *LeGallo 422* (MT).

United States. ALABAMA: Jackson Co., 6 Jun 1980, *Meigs 782* (UNA); Limestone Co., 20 May 1980, *Meigs 547* (UNA); Madison Co., 28 May 1980, *Meigs 661* (UNA); CALIFORNIA: Butte Co., 19 May 1988, *Oswald 3323* (CONN, WCSU); Humboldt Co., 9 Jun 1987, *Philbrick 2044* (CONN, WCSU); Napa Co., 29 Aug 1968, *Ackley s.n.* (CAS); CONNECTICUT: Fairfield Co., 20 Sep 1994, *Philbrick 4613* (CONN, WCSU); MARYLAND: Montgomery Co., 16 May 1942, *Killip 36567* (MO); Prince George's Co., 10 Jun 1943, *Hermann 10827* (NY); St. Mary's Co., 30 Sep 1984, *Philbrick 1386* (CONN, WCSU); Washington Co., 13 Jun 1981, *Hill 10318* (NY); MASSACHUSETTS: Barnstable Co., 2 Aug 1911, *Pennell 3381* (GH); Essex Co., 11 Jul 1957, *Harris 12997* (NEBC); Franklin Co., 25 May 1965, *Eaton & Eaton 5711* (NEBC); Hampshire Co., 7 Jun 1960, *Livingston s.n.* (NCU); Plymouth Co., 22 May 1980, *Sorrie 351* (NEBC); MONTANA: Stillwater Co., 18 Sep 1898, *Blankinship s.n.* (WTU); NEW JERSEY: Atlantic Co., 22 Feb 1937, *Long 49629* (PH); Bergen Co., 11 Jul 1891, *Nash s.n.* (NY); Camden Co., 20 Aug 1905, *Stone 7382* (PH); Cumberland Co., 12 Aug 1923, *Long & Bassett s.n.* (PH); Gloucester Co., 16 May 1910, *Long 3396* (PH); Hunterdon Co., 27 Jun 1972, *Roberts 2433* (PH); Mercer Co., 20 Jan 1885, *Peters s.n.* (PH); Middlesex Co., 17 Jun 1945, *Koster D16-23-3* (PH); Monmouth Co., 2 Sep 1923, *Beals & Bassett 7665* (CAS); Passaic Co., 31 May 1901, *Svenson 4478* (MU); Salem Co., 5 Jun 1932, *Long 37637* (OS); Somerset Co., 4 Jun 1945, *Chrysler s.n.* (PH); Union Co., 29 Jun 1936, *Kezer s.n.* (NY); Warren Co., 12 Aug 1949, *Shaeffer 31450* (PH); NEW YORK: * "Thusk" (?), Jul 1861, *J.G.B. 383* (F); Nassau Co., 15 Jun 1926, *Ferguson 2173* (NY); Orange Co., 27 Aug 1936, *Muenschler & Curtis 5746* (CU); Putnam Co., 23

Aug 1936, *Muenschler & Curtis 5745* (CU); Suffolk Co., 4-5 Jul 1898, *Clute 111* (NY); Ulster Co., 17 Jun 1926, *Ferguson 4879* (NY); OREGON: * 1871, *Hall 460* (F); Benton Co., 18 May 1980, *Halse 2162* (ARIZ); Clackamas Co., 13 Jun 1987, *Philbrick 2067* (CONN, WCSU); Clatsop Co., 20 Aug 1902, *Sheldon S.11215* (F); Coos Co., 11 Jun 1987, *Philbrick 2057* (CONN, WCSU); Douglas Co., 11 Jun 1987, *Philbrick 2059* (CONN, WCSU); Jackson Co., 11 Jun 1987, *Philbrick 2053* (CONN, WCSU); Lane Co., 12 Jun 1987, *Philbrick 2061* (CONN, WCSU); Lincoln Co., 15 Nov 1952, *Steward 6228* (CAS); Linn Co., 12 Jun 1987, *Philbrick 2063* (CONN, WCSU); Polk Co., 13 Jun 1987, *Philbrick 2066* (CONN, WCSU); PENNSYLVANIA: Bedford Co., 2 Sep 1939, *Berkheimer 1445* (PH); Berks Co., 19 Apr 1941, *Wilkins 6555* (PH); Bucks Co., 28 Aug 1923, *Long 29099* (PH); Carbon Co., 8 Jul 1951, *Wherry s.n.* (PH); Chester Co., 5 Jul 1924, *Long 31290* (PH); Cumberland Co., 30 May 1929, *Ward s.n.* (PH); Dauphin Co., 24 Jun 1952, *Berkheimer 13497* (PH); Delaware Co., 13 May 1911, *Eckeldt s.n.* (PH); Lancaster Co., 19 Jul 1948, *Fassett 27852* (PH); Lehigh Co., 8 Jul 1960, *Shaeffer 61135* (PH); Lycoming Co., 21 Jun 1955, *Wahl 15909* (PH); Montgomery Co., 15 Oct 1922, *Long 26781* (PH); Northampton Co., 28 Jul 1960, *Shaeffer 61498* (PH); Philadelphia Co., 17 May 1923, *Meredith s.n.* (PH); VIRGINIA: Fairfax Co., 25 May 1952, *Fosberg 34488* (RSA); WASHINGTON: Benton Co., Aug 1926, *Jones 369* (WIS); Cowlitz Co., 15 Jun 1987, *Philbrick 2071* (CONN, WCSU); Gray's Harbor Co., 6 Sep 1957, *Thorne 19122* (WTU); Jefferson Co., 20 Jun 1987, *Philbrick, Philbrick & Busse 2090* (CONN, WCSU); King Co., 28 Jul 1933, *Thompson 9612* (WTU); Kittitas Co., Sep 1965, *Spellenberg 1313* (F); Pacific Co., 15 Jun 1987, *Philbrick 2077* (CONN, WCSU); Pierce Co., 29 Apr 1934, *Jones 4620* (WTU); Thurston Co., 12 Jun 1942, *Meyer 2161* (MO); Wahkiakum Co., 15 Jun 1987, *Philbrick 2075* (CONN, WCSU); Whatcom Co., 15 Jul 1965, *Sutherland 1083* (WTU); Yakima Co., 15 Oct 1942, *Hoover 5998* (US); WISCONSIN: Dane Co., 13 Aug 1958, *Hartley 5322* (WIS); Monroe Co., 19 Aug 1956, *Hartley 2487* (WIS); Oneida Co., 25 Aug 1925, *Davis s.n.* (WIS).